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Diapause Initiation, Maintenance, and Termination Can Be Understood as Sequential Information-Processing Decisions in Insects

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ABSTRACT

Diapause is commonly described through its environmental triggers, endocrine regulation, and developmental consequences, yet these perspectives often treat initiation, persistence, and termination as partially independent phenomena. This article proposes that insect diapause can be interpreted as a sequence of information-processing decisions in which environmental signals are acquired, evaluated, retained through physiological state, and reassessed before developmental reactivation. The framework does not imply cognition or a universal computational mechanism; rather, it organizes evidence showing that different diapause phases rely on different environmental histories, physiological states, and regulatory processes. Evidence across insect taxa indicates that cue reliability, developmental stage, endocrine state, metabolic organization, and previous environmental exposure influence diapause transitions. The proposed framework separates evidence-supported biological processes from theoretical synthesis and identifies boundaries where prediction remains uncertain. This perspective provides a conceptual structure for integrating ecological signals with physiological mechanisms while highlighting experimental requirements needed to test phase-specific information processing in insects.

Keywords: Insect diapause, Seasonal cues, Photoperiodism, Physiological state memory, Endocrine regulation, Environmental uncertainty

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Introduction

Insect diapause is a complex developmental strategy involving arrested or modified development, altered metabolism, and coordinated physiological reorganization. Although diapause is often discussed as a response to seasonal adversity, available evidence indicates that it is not a single uniform state. Transcriptomic investigations have demonstrated that diapause progression can include distinguishable phases with different molecular profiles, suggesting that entry, persistence, and termination may involve distinct regulatory conditions rather than one continuous inactive state [1].

Seasonal timing has traditionally been examined through photoperiodic responses and circadian regulation. However, comparative analyses indicate that insects use diverse mechanisms for measuring environmental time, and no single timing architecture explains all diapause systems [2]. Molecular studies further demonstrate that clock-associated factors can influence diapause-associated traits in tissue- and species-dependent ways rather than acting as universal switches [3, 4].

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This article develops a theoretical framework in which diapause transitions are interpreted as sequential information-processing decisions. The term "information-processing" is used as an organizing analogy for biological processes: insects detect environmental variables, translate them into physiological states, maintain internal conditions over time, and reassess whether developmental continuation is appropriate. It does not imply neural computation, conscious evaluation, or a conserved algorithm.

The central problem addressed is that existing studies often explain individual components of diapause regulation while leaving unresolved how different phases integrate environmental history. A photoperiodic cue that contributes to initiation may not be the same signal that controls termination. Likewise, physiological changes that maintain diapause may represent retained internal state information rather than passive consequences of developmental arrest. The framework proposed here integrates these distinctions while preserving taxonomic, life-stage, environmental, and mechanistic boundaries.

Environmental inputs to diapause decisions

Environmental information enters diapause systems through multiple channels, including photoperiod, temperature, moisture, and environmental history. Photoperiod is a major seasonal cue in many insects, but its interpretation depends on biological context. Functional disruption of clock-related genes in *Bombyx mori* demonstrates that circadian components can be required for photoperiodic diapause induction in a particular system [5]. However, this finding should not be interpreted as evidence for a universal clock-controlled diapause mechanism across insects.

Environmental signals may also include information inherited from previous generations or earlier developmental conditions. In *Trichogramma telengai*, grandmaternal temperature exposure altered diapause induction responses under particular photoperiodic conditions, demonstrating that environmental history can modify later developmental decisions [6]. Similarly, experiments with *Anastatus japonicus* showed that temperature, photoperiod, and developmental stage interacted during diapause induction rather than acting as independent predictors [7].

These findings support a distinction between an external cue and the biological interpretation of that cue. The same environmental variable may have different consequences depending on developmental stage, physiological condition, and taxonomic context. A short photoperiod does not contain an intrinsic diapause meaning; rather, its significance emerges from the insect's regulatory system.

Human-modified environments further illustrate this distinction. Artificial light at night altered seasonal responses in *Culex pipiens*, demonstrating that anthropogenic changes can disrupt relationships between environmental signals and seasonal physiology [8]. Conversely, termination studies in *Sitodiplosis mosellana* indicate that environmental variables important during one phase may have limited influence during another, with chilling, moisture, and temperature affecting post-diapause progression differently from initiation cues [9].

Cue reliability and integration

Environmental cues are not equally reliable under all conditions. A central assumption of the proposed framework is that diapause decisions depend not only on signal detection but also on whether a signal accurately predicts future environmental conditions.

Experimental work in *Drosophila melanogaster* illustrates why cue interpretation requires caution. Apparent photoperiodic responses may be influenced by correlated thermal conditions, demonstrating that environmental experiments can unintentionally combine multiple information sources [10]. Geographic comparisons also show that diapause inducibility varies among populations, indicating that response characteristics cannot automatically be transferred across locations or genetic backgrounds [11].

The interpretation of diapause itself can also vary according to measurement strategy. Comparative work in *Drosophila* has shown that scoring methods and environmental conditions influence whether a phenotype is classified as diapause, emphasizing the importance of operational definitions [12].

Previous environmental exposure may further influence current responses. Studies of parasitoid systems indicate that transgenerational effects can occur but may depend strongly on population history and experimental context [6, 13]. Therefore, retained environmental information should be understood as conditional physiological history rather than as a universal inherited memory mechanism.

Initiation thresholds

The transition into diapause requires a shift from environmental perception to physiological commitment. Critical photoperiod provides a useful population-level description of when a proportion of individuals enter diapause under defined conditions, but it should not be interpreted as a universal individual threshold or a single internal switch [14].

Molecular studies reveal that initiation can involve multiple interacting regulatory pathways. In *Helicoverpa armigera*, signaling associated with ROS, AKT, S6K, CREB, and HIF-1 has been linked with diapause initiation, suggesting that commitment involves coordinated intracellular changes rather than one isolated trigger [15]. Additional work implicates TGF-β-related regulation of PP2A and Akt states during diapause entry in the same species [16].

Endocrine regulation also varies among insects. Studies of *Colaphellus bowringi* show that juvenile hormone-associated pathways, including Kr-h1 regulation and hormone biosynthesis, contribute to reproductive diapause regulation [17, 18]. However, endocrine pathways cannot be generalized without considering species and sex. Research in *Pyrrhocoris apterus* demonstrates sex-specific differences in diapause regulation, including divergent hormonal relationships between males and females [19].

These findings support a proposed interpretation of initiation as a threshold-like transition emerging from interacting environmental and physiological conditions. The threshold is not necessarily a fixed value but a context-dependent state in which multiple signals converge.

Information retention during maintenance

Maintenance represents the period in which an insect remains committed to diapause despite changing external conditions. The proposed framework interprets this stage as retention of physiological information: internal states generated during initiation continue to influence later responsiveness.

Evidence from the Asian longhorned beetle indicates that diapause maintenance can involve persistent developmental suppression, metabolic adjustment, and chilling-dependent progression rather than simple absence of activity [20]. Molecular studies further demonstrate that maintenance involves active regulation. In *H. armigera*, MEK/ERK-associated signaling contributes to maintenance of diapause state, although pathway roles remain taxon-specific [21]. Metabolic studies in *Chlosyne lacinia* similarly show that diapause involves temporal reorganization of biochemical processes rather than generalized metabolic shutdown [22].

Energy storage and post-transcriptional regulation provide additional examples of retained physiological state. In *Culex pipiens*, disruption of glycogen synthase affected storage patterns and survival-related outcomes during diapause, demonstrating a functional relationship between metabolic preparation and persistence [23]. In *Aedes albopictus*, microRNA profiles differed between induction and maintenance conditions, including a lack of differential abundance during induction but altered abundance during maintenance, emphasizing phase-specific molecular organization [24].

The following table addresses a question that prose alone cannot efficiently resolve: how different forms of retained physiological information alter interpretation of diapause maintenance without implying a universal memory mechanism.

Table 1. Distinguishing retained physiological information states during insect diapause maintenance and their interpretation boundaries

Maintenance state			Retention claim
Retained-information dimension	**Diapause phase and taxon**	**Persistence marker**	**Maintenance interpretation and reset test**
Persistent developmental state	Larval and pupal diapause systems	Continued developmental suppression under permissive conditions	Maintenance represents an active physiological state rather than simple inactivity. Evidence differs among taxa and diapause types. Test whether maintenance markers predict later transitions
Environmental history retention	Chilling-dependent species and seasonal systems	Previous temperature exposure alters later progression	Earlier conditions can modify future responsiveness. Does not indicate cognitive memory. Manipulate prior exposure while controlling current cues
Metabolic state retention	Mosquito and lepidopteran systems	Altered storage, metabolic rate, and	Internal resource state contributes to persistence. Specific pathways may not transfer across species. Compare phase-specific metabolic functions

		biochemical organization	
Molecular state persistence	Insects with transcriptomic, protein, or miRNA changes	Phase-associated regulatory differences	Maintenance can involve active molecular regulation. Molecular association does not always establish causal necessity. Combine functional manipulation with phase tracking
Proposed information-retention construct	Cross-taxon theoretical synthesis	Integration of phase-specific evidence	Provides a framework for explaining why previous states influence later transitions. Proposed model requiring validation. Test predicted state-history effects experimentally

Termination and reassessment

Termination requires insects to determine when continued dormancy is no longer appropriate. Evidence suggests that this transition is not simply the reverse of initiation. Instead, termination may involve reassessment of internal physiological readiness and external conditions.

In *Pieris napi*, endocrine responsiveness changed during diapause progression, with temperature and time influencing recovery of responsiveness to developmental hormones [25]. This suggests that termination can involve restoration of developmental competence rather than only detection of an external release signal.

Different physiological routes may also converge on similar outcomes. Studies of *Helicoverpa zea* demonstrated that different endocrine treatments terminating diapause produced overlapping developmental outcomes but partly different molecular responses [26]. Therefore, a common phenotype does not necessarily indicate a single underlying pathway.

Termination must also be distinguished from post-diapause development. Work on *Listronotus maculicollis* showed that chilling influenced diapause termination while reproductive maturation followed later, indicating that release from diapause and restoration of full developmental function are separate processes [27].

False positives and false negatives in seasonal prediction

Seasonal prediction requires an assumption that environmental information remains informative. However, the relationship between a cue and future conditions may become unreliable when environments change, when multiple cues become uncoupled, or when historical associations no longer reflect current conditions. These situations create the possibility of incorrect seasonal decisions.

In this article, false-positive and false-negative terminology is introduced as a proposed conceptual classification rather than as a measured error rate. A false-positive-type outcome refers to committing to diapause when subsequent conditions do not support the expected seasonal challenge. A false-negative-type outcome refers to insufficient diapause commitment or premature termination when unfavorable conditions remain. These categories organize possible mismatches between interpreted information and later environmental reality; they do not imply that insects consciously calculate probabilities.

Evidence from invaded environments illustrates how cue reliability may shift. In *Cydalima perspectalis*, termination responses in an invaded European population were more strongly associated with temperature than photoperiod under the tested conditions, suggesting that the relative importance of environmental variables may change across ecological contexts [28]. This finding does not demonstrate that the population has achieved an optimal strategy or that a specific response is universally advantageous. Rather, it demonstrates that environmental interpretation can be context dependent.

Other studies reveal mechanisms through which seasonal information can become unreliable. Artificial light at night can disrupt photoperiodic information [8], while thermal conditions can confound interpretations of photoperiodic responses [10]. Together with evidence from novel environments [28], these examples support the proposed idea that prediction errors can arise when environmental signals and ecological outcomes become disconnected. These relationships remain hypotheses about decision mismatch rather than quantified estimates of fitness cost or population-level failure.

A visual representation of this distinction is required because the central problem is not simply a sequence of events but a relationship between signal reliability, internal state, and possible interpretation error. **Figure 1** therefore organizes the proposed state-space logic of seasonal prediction under uncertainty.

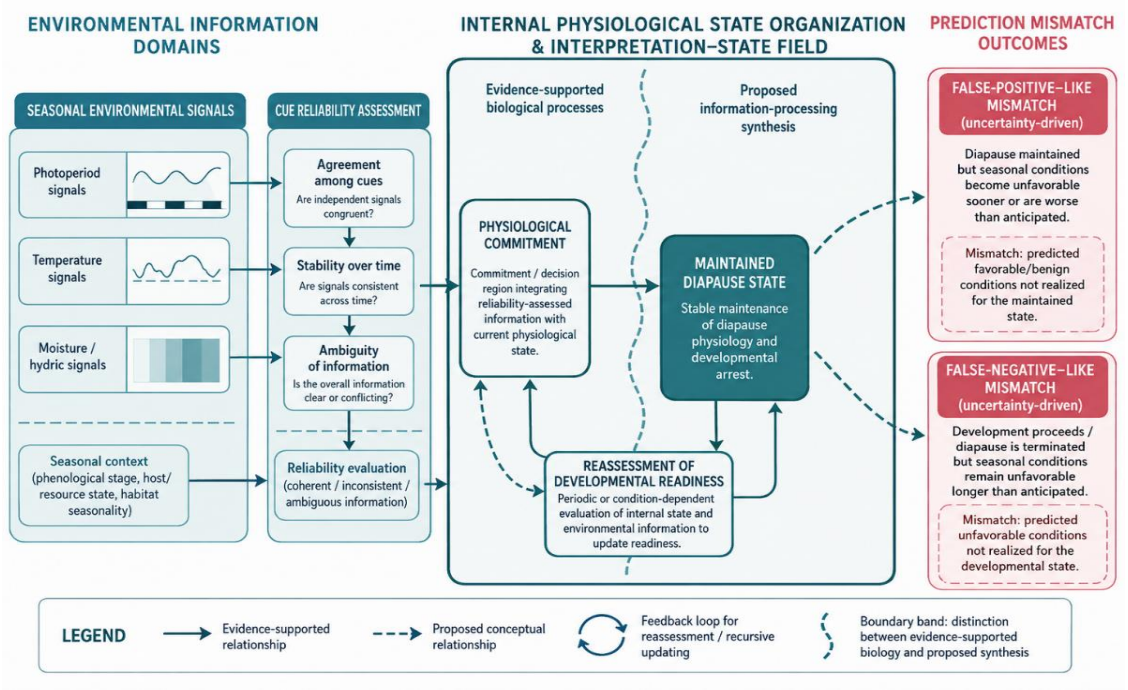


Figure 1. Seasonal information mismatch as a state-space problem in insect diapause prediction

Sequential information-processing model

The evidence reviewed above supports a conceptual shift: diapause can be interpreted as a sequence of phase-specific biological information-processing states. This interpretation does not claim that insects perform cognitive decisions. Instead, it proposes that different biological systems transform environmental information into different physiological consequences depending on timing, state, and context.

The first stage is environmental acquisition. Cues such as photoperiod, temperature, and developmental history influence whether an insect enters diapause. The second stage is commitment, during which endocrine and molecular systems establish a diapause-associated physiological condition. The third stage is maintenance, where metabolic and regulatory processes preserve that condition. The fourth stage is reassessment, where physiological readiness and environmental conditions interact to determine termination.

This sequence differs from a simple trigger-response model because the same environmental variable may have different meanings at different stages. A short photoperiod may contribute to initiation, while accumulated chilling or endocrine sensitivity may determine termination. Likewise, maintenance involves retained physiological conditions rather than merely continued exposure to the original cue.

The following table addresses the scientific problem of reconciling apparently conflicting diapause observations by separating evidence-supported phase functions from proposed transitions in the sequential information-processing interpretation.

Table 2. Reconciling phase-specific evidence within a sequential information-processing interpretation of insect diapause

Sequential phase	Input/state context	Observable transition	Information-processing role	Mistaken inference and decisive observation
Environmental acquisition state	Photoperiodic and thermally regulated insects	Cue-response experiments and population comparisons	Environmental signals provide context for diapause commitment	Cue importance differs among taxa and stages. Compare multiple environmental predictors simultaneously
Commitment transition state	Moths, beetles, bugs and parasitoids	Endocrine and signaling studies during entry	Initiation may emerge from interacting physiological conditions	No universal molecular threshold established. Test phase-specific regulatory combinations
Maintained state	Mosquitoes, beetles and lepidopterans	Metabolic, signaling and	Diapause persistence requires active physiological organization	Mechanisms are taxon-specific. Identify state markers that predict later transitions

		transcriptomic evidence		
Reassessment state	Butterfly, moth, weevil and midge systems	Hormonal responsiveness, chilling and emergence studies	Termination may involve restoration of responsiveness rather than simple cue reversal	Termination and post-diapause development differ. Separate release from later developmental recovery
Proposed sequential information-processing architecture	Cross-taxon synthesis	Integration of phase-specific evidence	Provides a framework linking environmental information with changing physiological states	Requires direct experimental validation. Manipulate previous states and measure later transition responses

The proposed framework therefore treats diapause as a sequence of changing biological interpretation states. It does not replace molecular, ecological, or evolutionary explanations; instead, it provides a structure for connecting them while preserving their boundaries.

Physiological predictions

The proposed framework generates several testable predictions. First, if diapause phases represent distinct information-processing states, biomarkers associated with initiation should not always predict maintenance or termination. Evidence that molecular signals differ among phases supports this possibility, although direct validation of the proposed architecture remains incomplete [24].

Second, internal physiological states should influence later responses to standardized environmental cues. Studies demonstrating effects of previous thermal exposure, chilling history, or developmental state provide examples consistent with this prediction [6, 20]. However, such effects should be interpreted as physiological history rather than cognitive memory.

Third, environmental information may be converted into endocrine states that influence future diapause outcomes. Maternal juvenile hormone regulation in *Nasonia vitripennis* provides a functional example in which environmental conditions are linked to offspring diapause fate through endocrine regulation [29]. This finding supports the plausibility of internal biological encoding of seasonal information, but it does not establish a conserved maternal mechanism across insects.

Future experimental approaches should test whether manipulated histories alter later transition responses, whether phase-specific biomarkers predict state changes, and whether the proposed sequential architecture applies across different diapause types. Such tests should include multiple taxa, life stages, and environmental contexts rather than assuming that one insect system represents all others.

Results and Discussion

The proposed information-processing perspective addresses a conceptual problem in diapause research: initiation, maintenance, and termination are frequently investigated separately despite being connected through changing biological states. Existing evidence demonstrates that diapause involves diverse environmental inputs, endocrine pathways, metabolic processes, and phase-specific molecular signatures [1, 2].

The framework contributes organization rather than a newly demonstrated mechanism. It integrates established observations into a proposed sequence in which insects acquire environmental information, establish physiological commitment, maintain internal state, and reassess conditions before developmental recovery. The value of this organization is that it preserves differences among mechanisms rather than forcing them into a single pathway.

Several limitations remain. First, the evidence base spans multiple insect orders and diapause forms. Reproductive diapause in adult mosquitoes, larval diapause in beetles, and pupal diapause in moths should not be assumed to share identical regulatory architectures. Second, laboratory studies frequently isolate individual variables, whereas natural environments provide interacting signals. Third, molecular associations require caution because expression changes do not automatically demonstrate functional necessity.

The framework also highlights unresolved evolutionary questions. It may be useful for generating hypotheses about how organisms respond when seasonal cues become unreliable, but it does not establish that any specific diapause response is adaptive, optimal, or fitness maximizing. Similarly, the proposed false-positive and false-

negative categories provide an interpretive vocabulary for seasonal mismatch but are not measurements of ecological failure.

Validation will require experiments specifically designed around sequential transitions. For example, studies could manipulate initiation conditions, maintain insects under controlled histories, and test whether later termination responses depend on earlier states. Such approaches would directly examine whether the proposed information-processing interpretation captures biological processes beyond descriptive analogy.

Conclusion

Diapause can be understood as a sequence of changing biological interpretation states in which environmental information is translated into phase-specific physiological responses. The proposed framework distinguishes environmental acquisition, commitment, maintenance, and reassessment while avoiding assumptions of universal mechanisms or cognitive decision making. Its primary contribution is conceptual: connecting ecological signals, physiological states, and transition boundaries into a structured model that can guide future experimental testing. The framework remains bounded by taxonomic diversity, environmental complexity, and the need for direct validation across insect systems.

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